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VARIATIONS IN THE CREST OF DAPHNIA HYALINA.

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THE characteristic tendency of Daphnia to form local varieties is expressed in *D. hyalina* by a variability in the cephalic crest, such that every kind of crest displayed in the genus may be observed in the species, which at the same time remains relatively constant in other distinguishing characters of *D. hyalina.* The object of this paper is a comparison between the American and the European forms, with a more careful inquiry into the conditions for several lakes offering widely different varieties.

My thanks are due to Professor E. A. Birge, of the University of Wisconsin, who furnished me with collections from northern Michigan and Wisconsin, and through whose kindness I had access to the literature on the subject; to Professor C. B. Davenport, of the University of Chicago, for many helpful suggestions in revising the results of my study; and to my brother, Karl E. Enteman, for assistance while collecting from southeastern Wisconsin.

Historical. — *D. hyalina* was first found by Leydig in the depths of the "Schlier See," and was given its name on account of its extremely pellucid character. Following are the chief points in its description as given in Leydig's *Naturgeschichte der Daphniden,* 1860: About as large as *D. longispina,* but somewhat narrowed, and at first sight distinguished from all known species by its extreme transparency; the head prolonged into a long, straight rostrum, without a ventral concavity, and so closely approximated to the thorax that the posterior outline is hidden between the valves of the carapace; macula nigra present; terminal claw smooth, showing under high power of microscope fine cross striations at base; the fornix much higher than in all known forms, the shell delicately sculptured into rhombs and prolonged posteriorly into a long dorsally directed spine (Fig. 1).

Observers subsequent to Leydig failed to find this species, but described forms which resembled it in all points excepting the form of the crest. The deviations here were sufficiently great to lead to their classification as distinct species. Such were *D. gracilis* Hellich, *D. pellucida* Müller, and *D. galeata* Sars; and not until recent years, when forms transitional between them and *D. hyalina* were found, have these come to be regarded as varieties of *D. hyalina.*

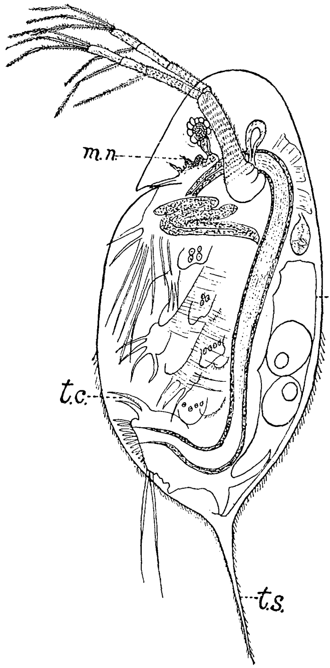

Fig. 1. — *Daphnia hyalina* Leydig; *m.n.*, macula nigra; *b.c.*, brood cavity; *t.c.*, terminal claw; *t.s.*, terminal spine.

Of *D. galeata*, Sars ('63) said: "It is distinguished from all other forms by the very characteristic development of its crest, which projects forward in an acuminate apex, giving the head a certain likeness to a helmet of the olden time. This singular projection undergoes noticeable variations in different localities. Sometimes it takes a direction straight forward, sometimes it is bent downward, and again it is very short, almost disappearing in adult females. In other localities the apex is highly developed, sabre-pointed, and in some even slightly recurved." The writer, however, fails to note a resemblance between any of these varieties and *D. hyalina.* In his résumé of the characters of *D. pellucida*, Müller ('68) makes mention of a pectinated terminal claw on the telson, which, if it is anything more than the fine striations noticed by Leydig, would serve to separate the two species; but later, in his "Cladoceres des Grand Lacs de la Suisses," he identifies Pellucida with Hyalina, since he found "all transitions between *D. hyalina* with a low even crest and terminal claw deprived of basal denticles, and *D. pellucida* with a large crest and a terminal claw ornamented at its base by a series of slight denticles." *D. gracilis* Hellich was distinguished from the foregoing mainly by its great height of evenly rounded crest, and was believed to be closely allied to *D. galeata.* Eylmann ('**86**) was the first to recognize the close relationship among the forms hitherto described. He classed them all as varieties of *D. hyalina.* Matile ('**90**) takes the same view. I translate from Eylmann:

"In the course of my work the conviction was more and more forced upon me that all Daphniæ possess a tendency toward the formation of local varieties, and indeed these variations are not limited to one part of the body, but extend to all parts; now it is the shape of the head, now the form of the valves, and again the size and development of the appendages, which give rise to the distinction as a variety. *However, the differences which arise in one habitat are very slight,* and extend to only a few individuals; but if we compare Daphniæ from separate localities, the differences are so striking that a doubt often arises as to whether the specimens are of the same or of different species, and often the question cannot be decided until transition forms are found in other localities which make possible a gradual change from one form to another." He cites *D. hyalina* as the best example of this character, and gives as a reason for these manifold deviations from the type the fact that the species is rigidly confined to lakes, the consequent isolation offering very favorable conditions for the origination of new forms. Richard ('**96**), in his "Revision des Cladoceres," included the above-mentioned forms, together with *D. plitvicensis* Sostaric[1] and *D. rectifrons* Stingelin,[2] in the single species *D. hyalina,* with the remark: "*D. hyalina* est d'ailleurs très variable, comme on le verra plus loin."

The American Representatives of the Species. — These have been but little studied. A brief description of two varieties found in lakes Wingra and Mendota was given in "List of Crustacea Cladocera from Madison, Wis.," by Professor Birge in 1875, while Herrick ('81) has described several forms which plainly belong to this species. Later observation led to the fact that "almost every lake possesses its own variety of *D. hyalina*"; and with this in mind Professor Birge, several years ago, gave me collections from a number of our lakes, and suggested that I study the different forms, their relations to one another and to the various European types. The material was all pelagic and collected from various parts of Michigan and Wisconsin. The lakes differ widely in character, from the small, reed-bordered Lake Wingra, or shallow Winnebago with its sandbars, to lakes like Mendota, of far greater depth, and whose shores slope from precipitous bluffs.

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[1] Low, rounded crest.

[2] Similar to var. *galeata.*

In general, the forms are remarkable for their close resemblance to the varieties of Europe, every variety but one being represented here; while several differ widely from any thus far described for Europe, but correspond in external appearance to the American representatives of widely different European species. Thus, while some European varieties of *D. hyalina* vary in the direction of the Kahlbergiensis, our forms vary to correspond with the American species Retrocurva and Breviceps. The transitions between the different types are sufficiently gradual to connect them with the original *D. hyalina* Leydig, thus seeming to confirm what has heretofore been, in a measure, assumed by other writers, — that the form first discovered is the one from which the others have departed. Following is a diagram (Fig. 2) representing the deviations from an assumed central form found in Lake Wabasis, Michigan, while the table on page 884 gives the principal characters in which the varieties are observed to differ. Each variety is named from the lake where it occurs.

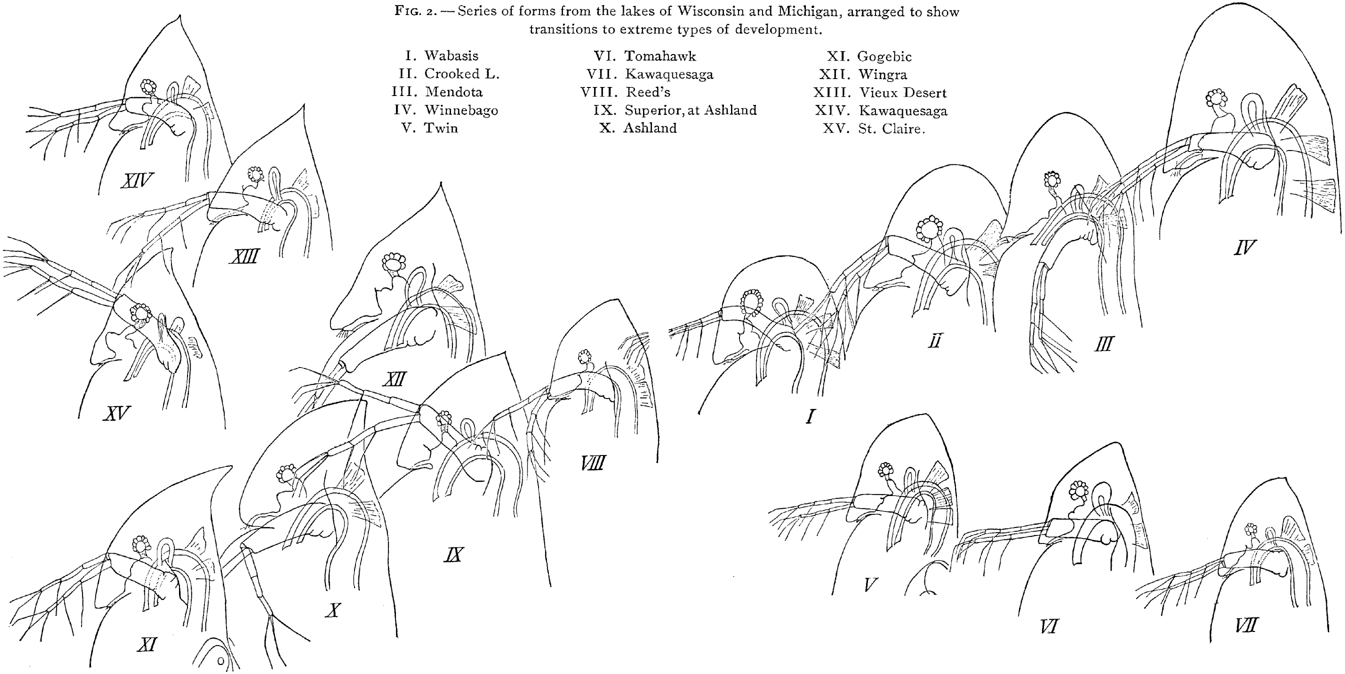

FIG. 2.—Series of forms from the lakes of Wisconsin and Michigan, arranged to show transitions to extreme types of development.

I. Wabasis
II. Crooked L.
III. Mendota
IV. Winnebago
V. Twin
VI. Tomahawk
VII. Kawaquesaga
VIII. Reed's
IX. Superior, at Ashland
X. Ashland
XI. Gogebic
XII. Wingra
XIII. Vieux Desert
XIV. Kawaquesaga
XV. St. Claire.

NAME.	CREST.	ROSTRUM.	ANTENNÆ.	SPINE.
Wabasis	Round, low, slightly narrower than carapace	Long	Basal joint curved, barely reaches margin of the head	Long, slightly upturned
Crooked	Little higher than the above-mentioned form	Long		
Mendota	Round, high, more than $\frac{1}{2}$ the length of carapace	Postero-ventral, ending in sharp point	Curved, slender, barely reaching margin	Very long, recurved postero-dorsally
Winnebago	Nearly $\frac{2}{3}$ length of carapace and as broad	Short, rounded	Slight, with short basal joint	Middle of lateral aspect, and a little longer than head
Twin	Pointed apex, dorsal to median line of lateral aspect	Rather short	Slight, with short basal joint	
Tomahawk	Apex somewhat more pointed than the foregoing	Rather short	Slight, with short basal joint	
Kawaquesaga, at Minocqua	Apex slightly acuminate	Rather short	Slight, with short basal joint	
Reed's	Antero-dorsal convexity prolonged into blunt apex	Short	Strong basal joint greatly curved	
Superior, near Ashland	Ventral line curved, dorsal straight or curved slightly upward	Extremely short and rounded	Basal joint nearly straight, and strong	
Gogebic	Elongated and strongly recurved	Long and blunt	Short and slight	
Wingra	Triangular, prominent subocular elevation	Short and blunt	Large and strong	Near median line of lateral aspect
Vieux Desert	About $\frac{1}{3}$ length of carapace, apex recurved	Long and blunt	Large and strong	
St. Claire	Dorsal and ventral curves marked, apex recurved	Rather long and rounded	Strong	
Kawaquesaga, at Minocqua	Dorsal and ventral curves marked, apex recurved	Rather long and rounded		

Types. — These numerous varieties may be classed under five types, three of which are quite the same as those described for Europe under the names Pellucida, Galeata, and Gracilis, while the other two are peculiar to our lakes. These are the St. Claire form, characterized by slight elongation and triangular shape of the head, and the Gogebic form, with greatly elongated and compressed shell, slender antennæ, and recurved apex of the crest. These two varieties differ most widely from the typical Hyalina, and at first sight appear to be entitled to specific rank. The most striking deviation is toward a form with pointed crest, the apex of which in European forms is ventral and in American varieties is dorsal to the median line of the lateral aspect. Further, the crested variety, as it occurs in Europe, approaches other European species, such as *D. kahlbergiensis*, while our recurved variety is very similar to *D. retrocurva*, the American representative of *D. kahlbergiensis*.

Range of Variation in One Locality. — In two localities only did this earlier material reveal the occurrence of more than one variety. In Lake Mendota two types may be distinguished, one closely resembling *D. gracilis*, the other the extreme round form of Lake Winnebago. Minocqua furnished forms approaching three widely differing types of development: (1) rounded crest, carried out into a sharp point; (2) extremely recurved apex; (3) triangular head with decided prominence over eye. Further examination, however, reveals a much wider range of variation for the single lake.

In the summers of 1896, 1897, and 1898, collections were made from a limited region in southeastern Wisconsin, known as the lake district of Waukesha County, and including about fifty lakes varying in size from the merest pond to those four or five miles in length and thirty meters deep. Thirty-five lakes were visited in all, most of them several times, but only fourteen of these have, up to the present time, yielded material in sufficient abundance for comparative study.

With a single exception these lakes furnish no new types, but in some lakes a single type with slight deviations is present, while others yield what might be considered distinct types, were it not for the occurrence of all imaginable transitions. This

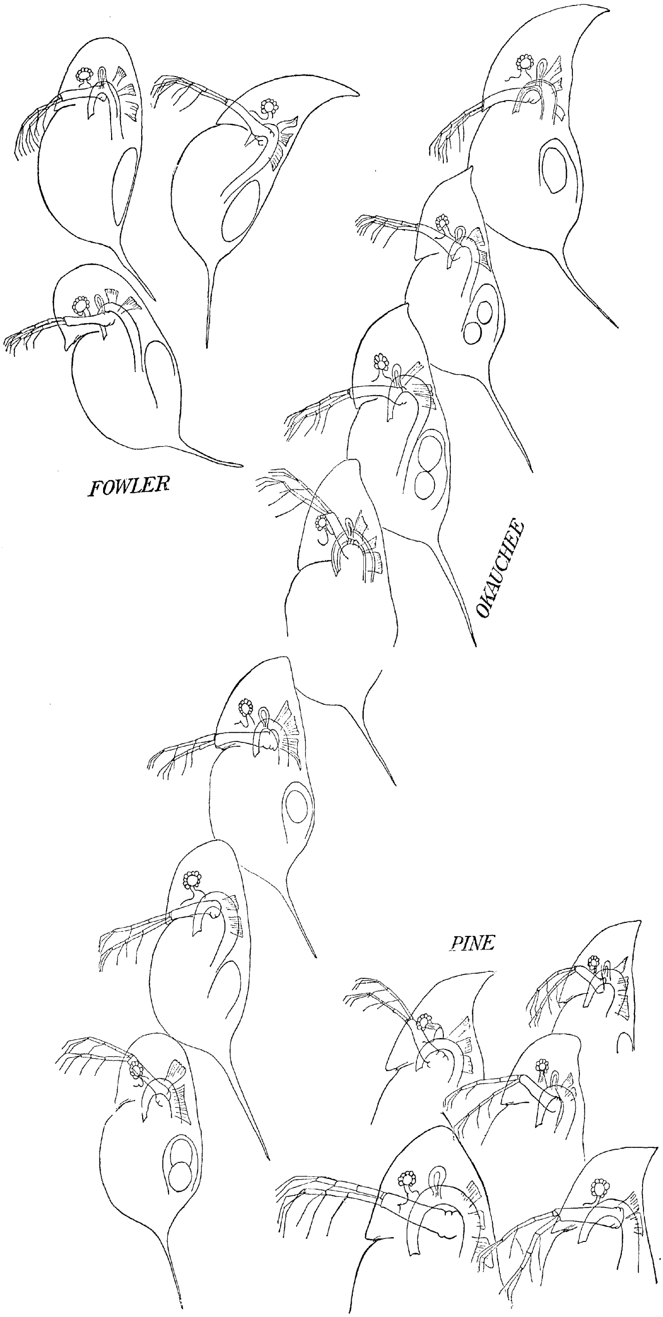

FIG. 3. — Series of forms showing range of variation for three lakes in southeastern Wisconsin.

is best shown by the accompanying series (Fig. 3), obtained in each case from single collections from Pine, Okauchee, and Fowler Lakes. It will be observed that in the two former every transition exists, from the low, evenly rounded to the extremely recurved and elongated crest, and the two series are seen to include all the American forms described, excepting perhaps the extreme of the triangular and the high-rounded types of development.

The amount of these variations was not uniformly great in all the lakes studied, nor for all the seasons in which collections were made. Thus, several collections taken from Beaver, one summer, showed the prevalence of a high-rounded crest with slight tendency to antero-dorsal angulation, while the following summer many crests exhibited a distinctly recurved apex. Lake Garvin, which communicates with Lake Okauchee by means of a channel having an approximate width of fifteen feet and depth of six feet, nevertheless appears to retain a

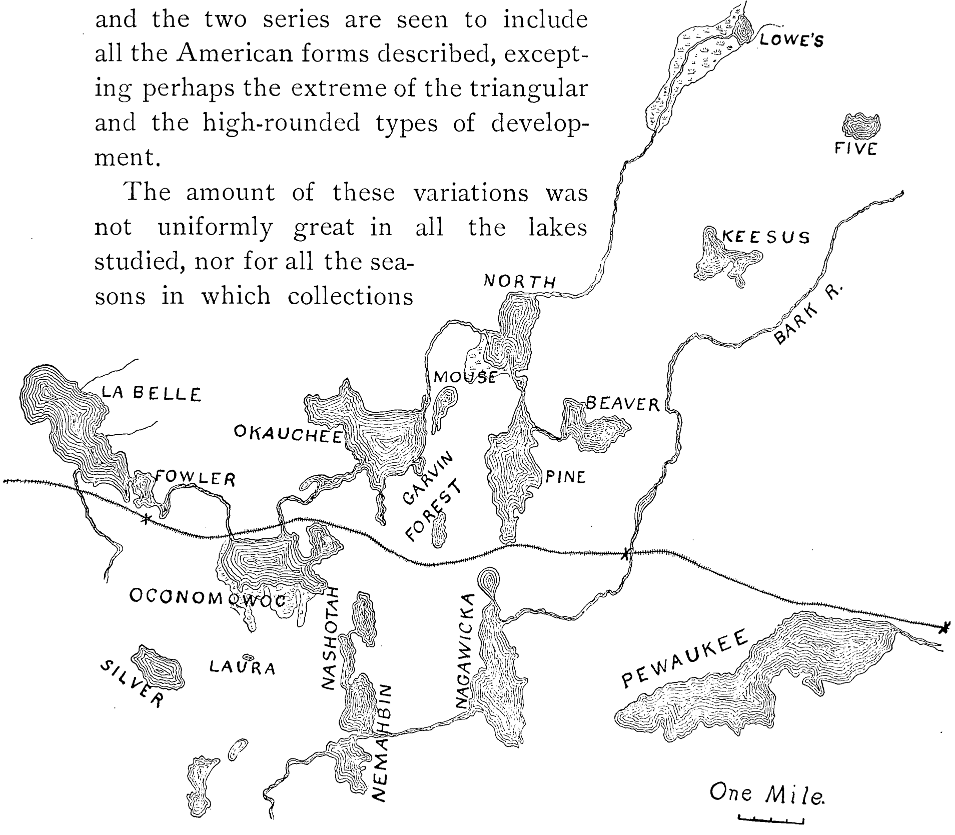

Fig. 4. — Map showing distribution of forms in southeastern Wisconsin. Taken from U. S. Topographical Survey. Lakes Laura and Garvin inserted by writer.

distinct type of crest. Lake Laura, in the immediate vicinity of Okauchee and Oconomowoc Lakes, and Lowe's Lake, which lies in the same system with these, show a uniform low-crested variety, while Lakes Five and Mouse exhibit the high-rounded type of crest, with marked subocular prominence. The accompanying map (Fig. 4) shows the greater part of the area in which these forms are distributed. The lakes of the Bark River system were very poor in Crustacea and furnished almost no Daphniæ.

Seasonal Variation. — More striking still is the fact that this range of variation is confined to the summer forms. Of course, owing to the difficulty of obtaining material in the winter, no very extended study of the winter forms has been made, but Professor Birge has for years made collections of winter forms from Lake Mendota, and I have his permission to state that they are uniformly low crested, while my own study of the winter forms of Lake Oconomowoc and Okauchee gives identical results. When it is remembered that the summer broods of Daphnia are produced parthenogenetically, the determination of the kind and conditions of variation must have an important bearing on questions of heredity and the origin of specific differences.

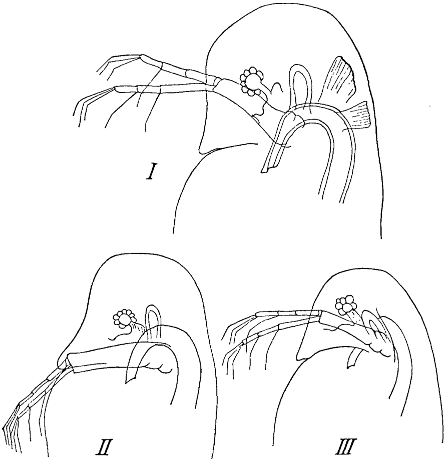

FIG. 5. — I, Lake Five; II, Mouse; III, Lowe's Lake form.

Correlations in Variability. — Although no quantitative study has yet been undertaken, careful comparison shows a direct relation between the length and curvature of the crest and the length and curvature of the terminal spine. The basal joint of the antennæ also varies, in size and strength, with the form and size of the shell. An attempt has also been made to relate the form of the crest with some character of the environment, such as depth and size of lake, temperature, etc., but thus far the attempt has been unsuccessful. Lakes widely different in character, such as Mendota and Winnebago, possess very similar forms, while some small shallow lakes produce such extremes as those of Lakes Laura and Henrietta (Fig. 6.) Again, the occurrence of a particular variation appears to bear some relation to the forms with which it is called upon to compete. Birge ('97), considering the occurrence of *D. hyalina* and *D. retrocurva* in Lake Mendota, states that one declined in numbers according as the other increased, and concludes this to be the result of active competition between the two species. My own much more limited observation indicates a competition in which certain variations are favored to the detriment of others. A more exact study of the quantitative differences, as well as a careful investigation of the environmental influences, will be made before we attempt to show the significance of these variations; but I think the facts as here given may serve to indicate the range of interesting problems offered by a generally accessible but little known form, and thus, perhaps, invite a more extended inquiry into the condition of the species in other localities.

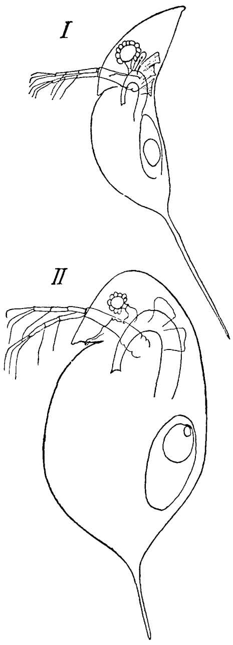

Fig. 6. — I, Form from Lake Henrietta; II, Lake Laura.

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